Plant Physiol. (1966) 41, 1065-1073

Orientation of Wheat Seedling Organs in Relation to Gravity[1]

Charles J. Lyon and Katsuyuki Yokoyama
Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire,
and
Ames Research Center, NASA, Moffett Field, California

Received March 30, 1966.

Summary. Seedlings of wheat (*Triticum aestivum* L.) were grown in special holders that permitted the coleoptile and early roots to develop in moist air. The orientation of the organs of seedlings erect to gravity was compared with that of organs produced on a horizontal clinostat. Orientation was described by the angular position of each organ tip with reference to the axis of the embryo. Comparative tests were also made with barley, rye, and oat seedlings.

The coleoptile of all species developed curvatures in 3 dimensions when geotropic responses were eliminated. The primary root was not precise in its positive geotropism. Seedlings grew on clinostats with much greater variations in the lateral orientation of the central root and with a tendency for it to curve away from the endosperm to a greater degree than in erect seedlings.

The symmetry of root system in wheat was found to depend on a specific mechanism. Under the influence of gravity the earliest lateral roots were oriented in a plane at characteristic angles of about 57.5° with the ideal primary root. The corresponding angles for lateral roots growing on clinostats were greater by about 47.5° as a result of epinasty not previously reported in roots. This force also appeared to be active in the seminal roots of barley and rye but not of oats.

The curvatures in coleoptiles grown without the directional effects of gravity correspond to the results of growth imbalance in *Coleus* stems in the absence of lateral transport of their auxin by gravity. Root epinasty appears to be based on auxin imbalance. Curvatures in the primary root are also interpreted as results of asymmetrical distribution of growth hormone.

The bilateral symmetry of a young wheat seedling contrasts sharply with the irregular form of seedlings of other small cereal grains. The coleoptiles are axial in all species but only wheat has a well-defined primary root flanked first by a pair of lateral roots that grow at equal angles and in approximately the same plane with the primary root. Later a second pair of seminal roots grow in the same plane and at nearly equal but larger angles with the primary root. These early roots of wheat seedlings are also essentially straight except as their forward growth is diverted by obstructions in the rooting medium.

Morphologists have described the variations and lack of symmetry in the seedlings of such grains as oats, rye, and barley (5, 13, 16). The first roots of species other than wheat exceed 3 in number and fail to show a pattern except that most of the early roots grow downward together. Their positive geotropic responses are so weak, however, that the root system spreads out in 3 dimensions just below the seed in any growth medium.

A tendency for the primary root of wheat to be slightly plagiotropic was observed by Rufelt (15) when he suspended the seedling with its roots in an aqueous medium. His photographs show this departure from the vertical after the root had grown nearly straight down for 1 or 2 cm. The result was a growth curvature toward the coleoptile side of the embryo although anatomy was disclaimed as a directional factor. Porodko (14) noted that the primary root of maize does not grow straight down in loose sawdust. Other writers (1, 7) have described irregular deviations from positive geotropic responses in seedling roots growing in moist air but no causes have been established for any such growth curvatures.

Recent demonstrations of the effect of gravity on the distribution of growth regulators (auxin) in coleoptiles (4, 6) and in the petioles (10), branches (9), and axis (12) of an upright plant suggest the possibility of comparable hormonal relations elsewhere, particularly within symmetrical root

[1] Supported by the National Aeronautics and Space Administration through research grant NsG-231 and research contract NAS2-1558.

systems. The need for correlating tropistic forces and growth regulators in a terrestrial plant starts with seed germination. For this investigation we used young wheat seedlings in which growth responses to gravity can be measured simultaneously for all their organs.

Methods and Materials

Seedlings of wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), rye (*Secale cereale* L.), and oats (*Avena sativa* L.) were grown in special holders and moist chambers for 3 or more days. The primary culture system was designed to germinate sets of 12 or 15 seeds held in tubes from which water, supported in a matrix of fine vermiculite, could enter the endosperm and thence move into the embryo (fig 1). As each seed germinated, the roots and coleoptile developed in air at 100 % relative humidity. The seeds were spaced to minimize contact of seedling organs with each other or with the plastic tubes that held the young plants, grown in darkness at 25 ± 0.5° to avoid phototropic reactions.

The seeds were sterilized chemically, washed, immersed for 4 hours in aerated water, and then inserted part way through holes in rubber membranes of the holder system (fig 1). The embryo end of the seed remained outside, with the radicle

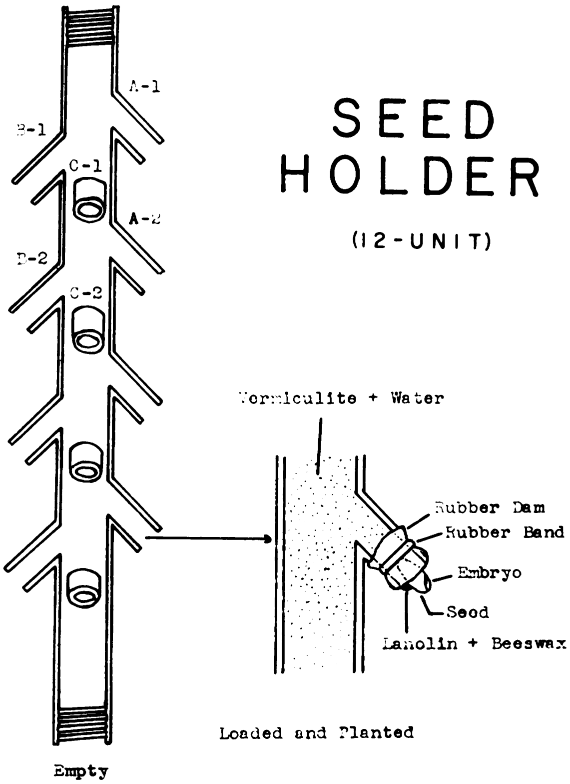

FIG. 1. Plastic holder system for culture of cereal seedlings in moist air of a sealed chamber.

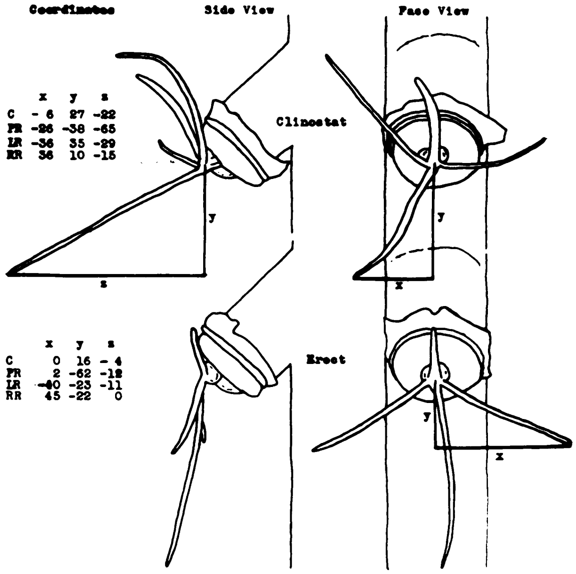

FIG. 2. Tracings of projected pictures of wheat seedlings and holder. Diagrams show method of obtaining coordinates for computing angular positions of organs. In data tables (of arbitrary units) C = coleoptile; PR = primary root; LR = left root; RR = right root.

pointing toward the end of the holder that was down when the seed was germinated in the erect position. These operations were carried out under lighting from cool white florescent lamps.

Growth responses to gravity in erect plants were eliminated in control experiments by rotating the germinating plants about their axes on a horizontal clinostat. The system of cylindrical moist chamber and multiple-seed holder was turned without vibration at 1 rph.

The orientation of coleoptile and roots in 3 dimensions was recorded by color photography and measured with dividers and scale from projections on a wall screen. The enlargement was 4.3 × natural size. As illustrated in figure 2, the face view of a seedling appeared in or was projected on the plane in which the 4 organs made their initial growth. Each one was oriented at a measurable angle with the vertical axis of the plant. The side view (fig 2), taken simultaneously with a mirror set at 45° to the axis of photography, showed a second angle which each organ made with the vertical axis if the organ grew out of the face-view plane, either away from or toward the camera.

The orientation of each seedling organ was described quantitatively by the 2 angles made with the plant's axis as they were displayed in the face and side views. Many variations in the root and coleoptile curvatures from plant to plant and along each organ made it practical to define each angle as that bounded by the vertical axis of the embryo and a line joining the tip and axial base of the organ. Face-view angles were measured clockwise from the vertical line above an erect embryo while side-view angles were measured from the 0° position of a coleoptile and from the down (180°) position of a root, the normal orientations for an upright seedling. Positive and negative values of these side-view angles were assigned as left and right, respectively, of the vertical axis because most curvatures of all organs were away from the endosperm side of a seed, hence left in the mirror image (cf. fig 2, 3).

Data for computing angles were obtained from the x, y, and z coordinates for the tips of each organ, measured from the 0, 0, 0 point on the vertical axis, as shown in figure 2. Measurements of angles in degrees were provided through a computer program, based on the arctan values of x/y and z/y.

Smaller numbers of wheat seedlings were also germinated in darkness in pots of mellow soil or on the surfaces of 2 % agar plates for 72 hours. Face-view angles for the plants grown in soil were measured directly after the roots were washed and allowed to spread freely in water. The corresponding angles for plants grown with the brush end of the endosperm embedded in a vertical sheet of agar were also measured directly from the seedlings.

Soil culture of seedlings could be used for erect plants only. The agar plate method permitted germination either in the erect position or on a clinostat that turned the seedlings at 1.5 rph. Time lapse pictures of germination in the 2 positions on agar were used for reconstructing growth sequences.

Experimental Results

Figures 2 and 3 show the usual forms of wheat seedlings as they grow with all organs free to develop in 3 dimensions, with and without a tropistic effect of gravity. Table I displays measurements of means of the 2 orientation angles, in face and side views, for the 4 organs in representative sets

Table I. *Sample Records of Mean Lengths and Orientation Angles of Wheat Seedling Organs after 72 Hours* Germination in holder system; angles in degrees; CO = coleoptile; PR = primary root; LR = left root; RR = right root.

Position	Seed no	CO mm	Face view	Side view	PR mm	Face view	Side view	LR mm	Face view	Side view	RR mm	Face view	Side view
Erect	12	9.0	4.7*	8.1	35.0	182.0	11.2	20.1	236.8	30.5	20.5	116.9	19.4
		±0.9	±0.8	±1.2	±1.4	±2.3	±2.7	±0.6	±1.4	±6.2	±1.0	±1.8	±5.5
Clinostat	15	9.7	7.5*	10.3	31.7	**	46.8	19.5	292.5	132.0	20.1	71.4	124.3
		±1.0	±2.3	±1.5	±1.1		±9.0	±0.9	±6.1	±11.1	±1.1	±5.8	±15.9

* Mean lateral curvature from erect position (0°).
** Mean is not significant; mean deviation from 180° = 46.8 ± 9.0° in contrast with mean deviation of 5.4 ± 1.7° for primary root of erect plants.

Table II. *Mean Orientation Angles of Seedling Organs*

Seedlings		Coleoptile Face*	Coleoptile Side**	Primary root Face	Primary root Side	Left root Face	Left root Side	Right root Face	Right root Side
Wheat									
Erect	130	3.8	+5.5	184.2	12.4	237.0	21.3	121.7	18.4
±SE		0.4	1.8	0.9	1.0	1.3	1.6	1.4	1.3
Clinostat	246	11.4	12.8		44.4	285.1	116.7	75.1	123.7
±SE		0.8	1.4		3.0	1.8	3.7	1.8	4.0
Barley									
Erect	24	4.4	+12.1	180.1	6.5	192.1	19.6	156.0	17.2
±SE		1.3	1.6	1.1	1.2	3.0	2.6	2.9	2.8
Clinostat	15	10.0	+26.1		66.7	257.7	77.9	79.5	95.7
±SE		3.0	3.2		12.7	13.3	10.6	9.3	16.9
Oats									
Erect	23	6.7	6.8	180.8	15.1	196.8	22.3	163.5	26.1
±SE		1.4	1.1	3.1	2.5	3.6	3.1	2.9	3.1
Clinostat	20	24.9	20.0		24.7	185.7	40.2	131.6	41.5
±SE		4.5	4.6		4.9	13.8	9.5	8.5	9.2
Rye									
Erect	20	3.7	3.6	182.9	7.3	193.2	12.3	164.7	13.6
±SE		0.9	1.2	2.8	1.4	4.7	2.9	4.2	3.1
Clinostat	14	15.4	9.9		52.0	254.3	78.5	129.5	79.9
±SE		3.8	1.7		11.9	10.2	13.2	22.3	13.5

* Angle measures the mean curvature from 0°, left and right.
** A plus value for a side-view angle shows that all curvatures were away from the seed holder.

of seedlings grown in the erect and clinostat positions for 3 days on seed holders. Table I also includes data for lengths of organs as they develop in moist air.

The means of angles for many experiments with 4 species, with and without geotropic growth responses, are shown in table II. The relatively small standard errors in these means for wheat seedlings emphasize the contrasting measurements for seedling form in the 2 positions of germination.

Coleoptile. When the wheat coleoptile reaches a length of 7 or 8 mm, it often fails to continue its straight growth even if it is erect to gravity. Curvatures to the right or left in face view are equally numerous but unbalanced growth rarely causes the tip to bend away from the embryo side of the seed, even when it germinates on a rotating clinostat. The outward growth curvatures are 2 or 3 times greater on the average (cf. table II) when the gravity vector is not alined along the axis of the organ, due in part to strong curvatures in a few seedlings of each set (cf. fig 3).

Primary Root. This central root of wheat commonly fails to have its tip straight down in erect plants; the position varies laterally by several degrees around a mean slightly greater than 180°. The root also tends to curve outward but seldom at an angle greater than 20° in the side view. Such displacement of a few degrees from the plant's axis is usually evident as soon as the root starts to grow (fig 3).

In the absence of gravitational force along the axis of the embryo, the primary root grows in an unpredictable direction. It often starts outward at an angle close to 90° with the plane of the embryo; later it may turn upward past the seed as seen in the face view. The usual result of germination on a clinostat, however, is a lateral position far from the 180° line (fig 3); the average deviation for the 246 seedlings of this report was 37.4 ± 4.1° as opposed to a corresponding lateral deviation of 7.9 ± 0.4° for the 130 seedlings that germinated erect to gravity.

As viewed from the side, the mean orientation angle for primary roots grown on a clinostat is close to 45° (cf. fig 3, table II), usually with about 20 % of them over 90° and very few of the root tips suspended on the seed holder side of the seed's axis. The average displacement of the root tip from the 180° position was over 3.5 times greater than when the seedling grew erect to gravity (cf. tables I, II, fig 3).

Lateral Roots. The first seminal roots of erect wheat seedlings differ greatly in orientation from those of seedlings germinated on a horizontal clinostat. Under the influence of gravity, these roots grow laterally at mean angles of 57 to 58° with the central root (as in fig 3). In the absence of gravity's directive effect, these characteristic angles are increased by 47 to 48° to form mean angles of about 75 and 105° with the 2 sides of the seedling axis (fig 3, table II). The symmetry tends to be preserved in each rotated seedling as the lateral roots grow faster on the sides that are lower when the plant is erect. Figure 3 illustrates the consistency of this growth response when the unilateral action of gravity is eliminated.

The side-view angles of these roots on an erect seedling average about 20° from the 180° position. Unlike the growth form of the primary root, however, the displacements of the lateral roots are distributed between the 2 sides of the plane of the embryo (cf. fig 3).

The corresponding side-view angles for seedlings grown on a clinostat are several times larger (tables I, II, fig 3). Most of the lateral roots of rotated plants curve outward from the plane of their origin. The relatively high standard errors for the average side-view angles indicate considerable variability in distribution of their growth regulators but the action of gravity seems to reduce the inherent imbalances to some extent.

Table III. *Effect of Culture Method on Size and Orientation Angles*

Wheat culture system	Coleoptile Mean length mm	Coleoptile Face* view Angle	Primary root Mean length mm	Primary root Face view Angle	Left root Mean length mm	Left root Face view Angle	Right root Mean length mm	Right root Face view Angle
Erect								
In soil	25.8	4.5	65.4	184.1	41.9	229.4	43.1	127.9
	±1.9	±0.9	±4.2	±2.3	±2.2	±2.0	±2.5	±2.8
In holders	6.4	3.8	30.4	184.2	17.4	237.0	17.2	121.7
	±0.4	±0.4	±1.3	±0.9	±0.6	±1.3	±0.7	±1.4
On agar	9.5	5.7	31.5	183.5	23.4	221.8	23.4	139.7
	±0.6	±0.9	±1.7	±1.7	±1.2	±2.3	±1.2	±1.7
Clinostat								
In holders	6.7	11.4	30.8	**	17.9	285.1	18.7	75.1
	±0.5	±0.8	±0.9		±0.5	±1.8	±0.6	±1.8
On agar	12.9	24.3	33.5	**	29.8	242.6	30.4	120.8
	±0.8	±3.9	±1.3		±1.4	±4.3	±1.2	±3.1

* Angle for coleoptile is mean deviation from 0°, not is not significant.

** Orientation is so variable that mean face-view anglemean orientation.

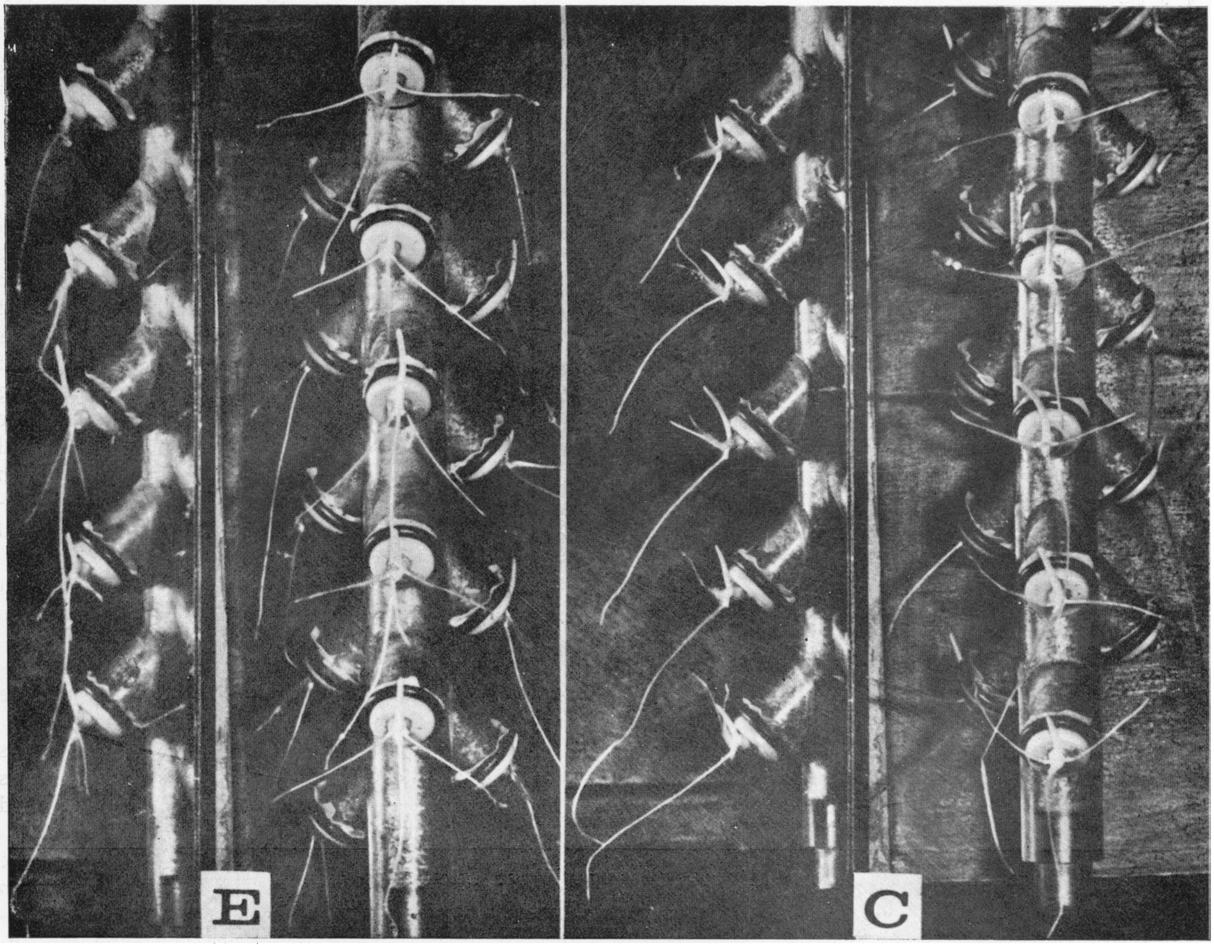

FIG. 3. Wheat seedlings after germination for 72 hours in erect (E) and horizontal clinostat (C) positions. Side-view images appear in 45° mirror at left of each face view.

Seedlings in Soil. The orientation of roots and coleoptiles of wheat plants grown erect in soil showed that seedling organs develop in moist air much the same as in soil. Table III includes data on organ length and mean face-view angles for 30 wheat seeds germinated in soil for 3 days. Seedlings of this age in plastic holders were much smaller but the organs grew at essentially the same angles with their seedling axes when all plants were upright.

Seedlings on Agar. Germination in moist chambers over agar produced erect plants with organs slightly longer than those of seedlings grown in plastic tube holders (table III). The important differences in form of seedlings appeared in the angles between the central and lateral roots. These angles were smaller than for either of the other methods of culture; yet the roots developed free in the moist air as they did in the special holder method in which the lateral roots grew at slightly greater angles with the central root than in the soil method.

The coleoptiles and lateral roots of seedlings grown on clinostats were much longer when they grew near agar than when they were supplied with water from plastic tubes. The orientation of organs was also different in agar-grown plants. The greater mean curvatures in the coleoptiles were associated with longer shoots in agar culture. The failure of the lateral roots of the erect and clinostat plants to differ in mean orientation angles by more than about 20°, as opposed to differences more than twice as large when grown in plastic holders, may be significant; the smaller increments in angular position of the lateral roots when the seedlings grew on clinostats are correlated with the smaller angles between these lateral roots and the central root when the wheat seedlings germinate erect on agar.

Alternation of Growth Position. Tests to distinguish between a possible effect of gravity on the angle of emergence of wheat roots and the lateral transport of auxin by gravity within elongating roots (2) were conducted by permitting only about half of the 3-day germination to take place either erect to gravity or on a clinostat. The root elongation was completed with the set of seedlings in the alternate growth position. Significant changes in orientation of the root tips after the change in position would reflect a gravitational effect during the elongation process.

The orientation angles of each root were measured from photographs taken after 38 hours of germination in the first position and a second set of photographs taken at the close of the 72-hour experiment. The results from 17 such tests, each with 12 or 15 seeds at the start, are shown in table IV.

The position of the primary root could not be altered much by growth in a second position since about two-thirds of the elongation had been completed before the shift. The most significant change was that produced in the mean side-view angle of about 55° after initial growth on the clinostat; during later growth in the erect position, the root tips grew downward enough to reduce greatly this angle of displacement from the seedling axis. The lateral deviations in the face-view angles were also smaller in erect plants.

An effect of gravity during the elongation period appears clearly in the data for both face- and side-view angles of the lateral roots. For change of growth position either from erect to clinostat or vice versa, the face-view angle between the root and a 180° orientation line was larger when the seedlings had just been growing on a clinostat. The side-view angle increased sharply if the shift was made to the clinostat and decreased when the plants were set erect to gravity after rotation in the horizontal position.

Tests With Other Species. From a limited number of tests with 3 other grains germinated in the plastic holders, the seedling organs of barley, oats, and rye were found to exhibit some differences from wheat in their orientation. The records of mean angles in table II include data for a central root and the 2 lateral roots with tips farthest from the seedling axis. Means for the face-view angles of the primary root were computed only for erect seedlings, as for wheat, because the position of its tip is always variable on a clinostat and the average face-view angle is seldom significant.

The data for barley seedlings resemble those for wheat except for the greater variability in the orientation angles of the roots. The coleoptile shows a greater tendency to grow faster on the side nearest the endosperm. The central root grows on

Table IV. *Effect of Gravity on Orientation Angles of Wheat Roots*

Growth positions	Erect ⟶	Clinostat	Clinostat ⟶	Erect
Hrs of growth	38	34	38	34
Primary root face view	182.2 ± 1.4	184.7 ± 2.4	171.3 ± 5.4	171.7 ± 4.0
" " deviation*	10.0 ± 1.0	14.6 ± 1.9	42.3 ± 3.7	30.5 ± 2.9
" " side view	21.4 ± 1.6	21.4 ± 2.9	54.6 ± 2.9	39.8 ± 2.4
Left root face view	244.1 ± 1.2	257.8 ± 2.5	275.9 ± 2.0	252.2 ± 1.6
" " side view	12.1 ± 2.1	63.2 ± 5.5	96.5 ± 5.9	46.6 ± 3.5
Right root face view	117.1 ± 1.1	105.8 ± 2.4	87.3 ± 1.5	109.5 ± 1.5
" " side view	15.3 ± 2.1	53.5 ± 5.2	96.4 ± 6.8	41.5 ± 3.5

* Deviation from 180° in face view.

the clinostat at a 50 % greater side-view angle with the 0 to 180° axis of the embryo. Although the 2 lateral roots do not grow at equal or characteristic angles on erect plants, the 66° increase in the mean face-view angle for the left root (table II) and the 76° reduction in the mean angle of the right root as they develop on a clinostat greatly exceed the corresponding responses (47–48°) of wheat to this physical condition. There seems to be some adjustment to gravity in growth regulation throughout the seedling.

Rye seedlings grown erect or on a clinostat are much like those of barley but there are quantitative differences in the coleoptile side angles and in the changes in position of the lateral roots when they grow on a clinostat. The angular position of oat roots, other than the central one, varies considerably but there is little or no difference between the means of their orientation angles on erect and clinostat seedlings. Only in the strong curvatures of coleoptiles on clinostats do oats show an important effect of gravity in the orientation of seedling organs.

Discussion

The frequent curvatures in coleoptiles of the 4 species grown on horizontal clinostats correspond to the unbalanced growth reported in 1962 (8) for stems of many *Dicotyledonous* plants in the absence of gravitational force along their axes. Curvatures under the same conditions have since been observed in stems of corn and lily and have been shown by quantitative work with *Coleus* (12) to be due to an imbalance of auxin delivered to the curved tissues.

It is well established that IAA, the auxin found in and used for the radiocarbon tracer work with *Coleus* stems, is the predominant growth hormone in coleoptiles. When Goldsmith and Wilkins (4) and Hertel and Leopold (6) reported on lateral transport of IAA by gravity in corn coleoptiles, they noted the similarity of the lateral and longitudinal transport mechanisms. The work on *Coleus* (12) demonstrated the action of gravity in maintaining an even distribution of IAA in axial tissues during basipetal transport. The coleoptile curvatures of this report amount to bioassays of imbalance in their endogenous auxin supplies when the action of gravity on basipetal transport is eliminated. More rapid growth on the endosperm side of the coleoptile, the cause of most of the side-view curvatures, may be related to a source of the auxin precursor in the endosperm.

The tendency of most primary roots of wheat seedlings to grow slightly faster on the side nearer the embryo's axis when the plant is erect becomes significant in the light of the much larger orientation angle of the side view when the effect of positive geotropism is removed on the clinostat. A possible explanation for both effects is that there is such an excess of auxin supplied to the outward side of the very young root that the force of gravity is insufficient to equalize the amounts present in the zone of elongation; when gravity is prevented from acting as an equalizing factor, the root grows even faster on the side nearer the embryo's axis.

The lateral orientation of the seminal roots of erect wheat at characteristic angles, in contrast with the consistently different positions when geotropic responses are prevented, corresponds closely to the behavior of herbaceous branches as in *Coleus* (9). The excess auxin delivered to the morphologically upper half of a branch, with part of the IAA transported laterally by gravity (11), provides for auxin balance at a characteristic angle on an erect plant but causes epinastic curvature on a clinostat because the upper side then grows faster. The normal angle of a lateral root seems to be due to the same auxin balance if the seedling is erect to gravity, but by analogy with the auxin distribution described earlier (2, 3) for positive geotropism in roots, the excess (unmeasured) on the upper side when the seedling is rotated around its axis leads to greater growth on the lower side. The result is root epinasty, not previously reported.

The epinastic curvatures of lateral roots are reflected in the 6-fold increase (table II) in the mean value of the side-view angle for a seedling grown on a clinostat; a different imbalance in growth causes the root tip to be placed outside the plane of the 2 roots. Since the curvature which thus displaces the root tip to either side of this plane appears in both erect and clinostat seedlings, it probably represents variable imbalance in growth of suspended roots, imperfectly controlled by gravity in erect plants and uncontrolled by it on a clinostat.

The symmetrical root system of wheat seedlings makes them the best subjects for study of the relation between gravity and growth regulators in grass seedlings but wheat is not a special case for these relationships. Barley and rye differ from wheat only in the degree to which they exhibit coleoptile curvatures, imperfectly positive geotropism in a pseudoprimary root, and root epinasty of lateral roots. Oat coleoptiles grow faster and have greater imbalances in growth rate in the absence of a directional effect of gravity but the roots of oat seedlings show a limited dependence on gravity for their growth regulation.

Acknowledgments

The plastic seed holder system for this work was developed in cooperation with Drs. Betty F. Edwards and Stephen W. Gray of Emory University and Drs. Herbert M. Conrad and Samuel P. Johnson of the Life Sciences Department of S&ID of North American Aviation, co-experimenters for the wheat seedling experiment in NASA's Biosatellite Project.

Literature Cited

1. Bennet-Clark, T. A., A. F. Younis, and R. Esnault. 1959. Geotropic behavior of roots. J. Exptl. Botany 10: 69–86.
2. Boysen-Jensen, P. 1933. Die Bedeutung des Wuchsstoffes für das Wachstum und die geotropische Krümmung der Wurzeln von *Vicia faba*. Planta 20: 688-98.
3. Boysen-Jensen, P. 1936. Über die Verteilung des Wuchsstoffes in Keimstengeln und Wurzeln während der phototropischen und geotropischen Krümmung. K. Danske Videnskab. Selskab Biol. Meddelelser 13: 1–31.
4. Goldsmith, M. H. M. and M. B. Wilkins. 1964. Movement of auxin in coleoptiles of *Zea mays* L. during geotropic stimulation. Plant Physiol. 39: 151–62.
5. Hector, J. M. 1936. Introduction to the Botany of Field Crops, Vol. I. Cereals. Central News Agency, Johannesburg.
6. Hertel, R. and A. C. Leopold. 1963. Auxin relations in geotropism of corn coleoptiles. Naturwissenschaften 50: 695–96.
7. Holman, R. M. 1916. The orientation of primary terrestrial roots with particular reference to the medium in which they are grown. Am. J. Botany 3: 274–318.
8. Lyon, C. J. 1962. Gravity factor for auxin transport. Science 137: 432–33.
9. Lyon, C. J. 1963. Auxin factor in branch epinasty. Plant Physiol. 38: 145–52.
10. Lyon, C. J. 1963. Auxin transport in leaf epinasty. Plant Physiol. 38: 567–74.
11. Lyon, C. J. 1965. Auxin transport in geotropic curvatures of a branched plant. Plant Physiol. 40: 18–24.
12. Lyon, C. J. 1965. Action of gravity on basipetal transport of auxin. Plant Physiol. 40: 953–61.
13. Mirbel, M. 1809. Nouvelles recherches sur les caractères anatomiques et physiologiques qui distinguent les plantes monocotylédones des plantes dicotylédones. Ann. Mus. d'Hist. Nat. 13: 54–86.
14. Porodko, Th. M. 1924. Über den Diageotropismus der Hauptwurzel bei Maiskeimlingen. Ber. Deut. Botan. Ges. 42: 405–19.
15. Rufelt, H. 1957. Influence of the composition of the nutrient solution on the geotropic reactions of wheat roots. Physiol. Plantarum 10: 373–96.
16. Sargent, E. and A. Arber. 1915. The comparative morphology of the embryo and seedling in the *Gramineae*. Ann. Botany 29: 161–222.